COMMUNITY ECOLOGY 1(1): 89-94, 2000
1585-8553 © Akadémiai Kiadó, Budapest

Quantifying the network connectivity of landscape mosaics: a graph-theoretical approach

C. Ricotta[1,2], A. Stanisci[1], G. C. Avena[1] and C. Blasi[1]

[1]*Department of Plant Biology, University of Rome "La Sapienza", Piazzale Aldo Moro 5, 00185 Rome, Italy.*
[2]*Corresponding author. Tel.: +39-06-49912408; Fax: +39-06-4457540; E-mail: cricotta@uniroma1.it.*

Keywords: Graph theory, Harary index, Palmarola, Reciprocal distance matrix.

Abstract: Connectivity determines a large number of ecological functions of the landscape, including seed and animal dispersal, gene flow and disturbance propagation, and is therefore a key to understanding fluxes of matter and energy within land mosaics. Several approaches to quantifying landscape connectivity are possible. Among these, graph theory may be used to represent a landscape as a series of interconnected patches, where flows occur as a result of structural and/or functional patch connectivity. Within this context, we propose the use of a graph-theoretic index (i.e., the Harary index) as a measure of landscape connectivity. Results derived from the analysis of the vegetation map of Palmarola (central Italy) show that, from a statistical and ecological viewpoint, the Harary index may be a better measure of landscape connectivity than more traditional indices derived from transportation geography.

Nomenclature: Pignatti (1982).

Abbreviation: TI - topological index.

Introduction

The concept of connectivity has long been used in transportation geography (Taaffe and Gauthier 1973), and more recently in landscape ecology for understanding and modeling flows of matter and energy within landscape mosaics (Risser et al. 1984). Landscape patches are connected depending on whether there are patterns or processes to link them in some way. Connections between patches arise either from static configurations (e.g., patch adjacency or soil distribution) or from dynamic processes, such as dispersal or disturbance (Green 1994). Furthermore, functional connections between landscape patches clearly change as a function of the process under consideration (Noss 1991). For example, patches that are connected for seed dispersal of anemochorous plant species may not be connected for zoochorous plant species or for animal movement (Grashof-Bokdam 1997, Green 1994).

Connectivity determines a large number of ecological functions of the landscape, including seed dispersal and colonizing ability (Grashof-Bokdam 1997, Grashof-Bokdam et al. 1998), animal dispersal (Johnson et al. 1992, Schippers et al. 1996, Schumaker 1996, Beier and Noss 1998), gene flow (Green 1994), fire spread and disturbance propagation (Turner et al. 1989, Green 1989) and soil erosion (Davenport 1998). Several approaches to modeling fluxes through a land mosaic, e.g., percolation theory (Milne et al. 1996, Keitt et al. 1997) or cellular automata (Couclelis 1985) are possible (Cantwell and Forman 1993). Within this context, graph theory (Harary 1969) is an effective way for reducing the complexity of landscape patterns into an understandable set of spatial configurations creating an universal framework for modeling landscape fluxes at any scale of observation (Cantwell and Forman 1993, Keitt et al. 1997).

Graph theory is commonly used in numerous research fields, such as transportation geography, pharmacology and microelectronics, to describe structural relationships between objects. In ecological research, graph theory has been principally used to analyze food webs (Cohen 1978, Cohen et al. 1990, Sugihara 1984) and vegetation dynamics (Dale 1985, Roberts 1989, Acosta et al. 2000). Recently, Johnson et al. (1998) used a multiscale topological approach to investigate the spatial distribution of breeding birds' species richness in Pennsylvania.

Mathematically, an (undirected) graph $G = (V, X)$ is composed of a finite set V of vertices together with a prescribed set X of unordered pairs of distinct elements of V, the elements of X being defined as edges. Focusing on thematic maps, such as vegetation or land cover maps as a

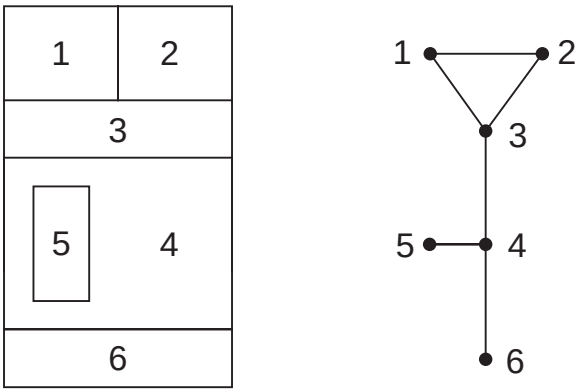

Figure 1. Artificial land cover map along with its corresponding landscape graph. Vertices represent landscape patches and edges represent adjacency among landscape patches. The labeling order of landscape patches and graph vertices is arbitrary.

surrogate of the real landscape, a landscape graph representing the spatial relationships among landscape patches may be obtained by mapping all vegetation patches as vertices, while the edges $x_{ij} \in X = (v_i, v_j)$, represent their adjacency (Keitt et al. 1997). That is, any two vegetation patches that share a common boundary are connected by an edge (Figure 1). Notice that, in anthropic landscapes, contacts at corners between landscape patches, such as agricultural fields are very common (Cantwell and Forman 1993), and we think they should be considered as well as contacts along segments. Following this simple rule, a landscape graph may be constructed from any thematic map at any scale of observation.

In this paper, we introduce a graph-theoretic index of network connectivity (i.e., global landscape connectivity) based on the construction of reciprocal distance matrices from landscape graphs. As an application for demonstration, the artificial graph of Figure 1 and an actual landscape graph derived from the vegetation map of the island of Palmarola (central Italy) were used.

Data

The island of Palmarola (136.36 hectares) belongs to the Pontine islands archipelago, located in the Thyrrenian Sea, about 30 km off the Italian peninsula (40° 51' N; 12° 58' E). The maximum elevation is 249 m above sea level. From Pliocene to lower Pleistocene, the archipelago was built by the eruption mainly of silicic magmas (trachytes, rhyolites and more recently basalts) on top of Meso-Coenozoic sedimentary and metamorphic bedrocks (Cosentino et al. 1993). Climate is of Mediterranean type, with annual total rainfall of 649 mm, mainly limited to autumn-winter period, and annual average temperature of 16.6 °C (Blasi 1994). Climatic data came from the meteorological station of Ponza Campo Inglese (185 m above sea level).

While there have never been permanent urban settlements on the island, the vegetation landscape of Palmarola is the result of widespread deforestation for vineyard cultivation and goat grazing. As a consequence, the prevalent vegetation types are *Cistus* spp. and *Erica multiflora* maquis, and *Genista thyrrena* and *Euphorbia dendroides* garrigue. Secondary therophytic grasslands with *Brachypodium ramosum*, and coastal cliff communities with *Helychrisum litoreum, Limonium pontium* and *Crithmum maritimum* are also quite common. *Erica arborea* maquis and *Quercus ilex* woods can be found just in the shelter sites on northern slopes previously occupied by vineyard terracing. From the vegetation map of Palmarola (Stanisci and Pezzotta 1992), the corresponding graph was generated (Figure 2).

Methods and discussion

In the last 50 years, several graph-invariant indices have been suggested to quantitatively describe the essential aspects of network connectivity based on graph topology (structure). A graph-invariant index yields the same value for all isomorphic graphs. Graph isomorphism is defined in terms of changes in the assignment of labels to the vertices. Such changes do not change the topology and two isomorphic graphs G_1 and G_2 are therefore "identical" as far as most graph-theoretical properties are concerned (Harary 1969).

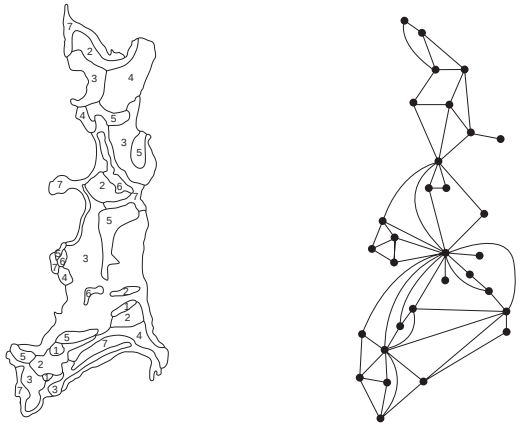

Figure 2. Vegetation map of the island of Palmarola along with its corresponding landscape graph. 1: *Quercus ilex* woods; 2: *Erica arborea* maquis; 3: *Cistus* spp. and *Erica multiflora* maquis; 4: *Genista thyrrena* and *Euphorbia dendroides* garrigue; 5: Therophytic grasslands with *Brachypodium ramosum*; 6: *Arundo donax* communities; 7: Coastal cliffs communities with *Helychrisum litoreum*, *Limonium pontium* and *Crithmum maritimum*.

Analytic representations of graphs may be constructed from landscape graphs to more fully understand the connectivity of elements. To obtain analytic representations of graph structure, the principal tools are the corresponding adjacency matrix $\mathbf{A}(G)$ and the distance matrix $\mathbf{D}(G)$. For a landscape graph G with N vertices, $\mathbf{A}(G)$ is a square $N \times N$ matrix (Basak et al. 1987) with elements a_{ij} defined as:

$$a_{ij} = \begin{cases} 1 \text{ if vertices } i \text{ and } j \text{ are adjacent in } G \\ 0 \text{ otherwise} \end{cases} \quad (1)$$

Conversely, the distance matrix $\mathbf{D}(G)$ of a graph G with N vertices is a square $N \times N$ matrix with elements d_{ij} indicating the topological distances in the graph. The topological distance d_{ij} between two vertices i and j is the number of edges along the shortest path between these two vertices (Figure 3).

For undirected landscape graphs without loops, both matrices are symmetric with zero elements in the main diagonal. Furthermore, graphs represented by adjacency or distance matrices are invariant to all permutations of the rows or columns of the matrices. Thus, if G is a graph with N vertices, there are $N!$ equivalent graphs corresponding to the number of ways the N vertex labels can be permuted. To uniquely characterize the structure of a graph, *topological indices* (TI), i.e., graph invariant reduced forms of adjacency or distance matrices are used (Basak et al. 1987). For example, a simple way to compute a local vertex invariant (i.e., a topological index associated to a single graph vertex) from the adjacency matrix of a graph is to add all a_{ij} elements along row i or column j of the matrix. This results in a vector whose elements v_i, called the degree of vertex i in graph theory or beta index in transportation geography represent the total number of edges connected to vertex i.

Besides beta connectivity, in landscape ecological applications of graph theory it may be useful to use the distribution of cutnodes in the analysis of landscape connectivity. Some connected graphs (i.e., graphs where every

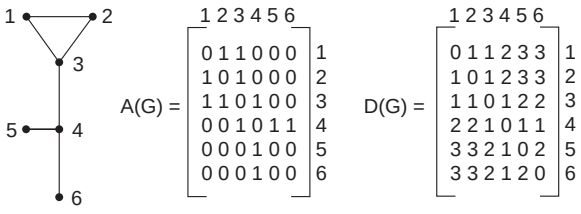

Figure 3. Example calculation of the adjacency matrix $\mathbf{A}(G)$ and the distance matrix $\mathbf{D}(G)$ for the landscape graph of Figure 1.

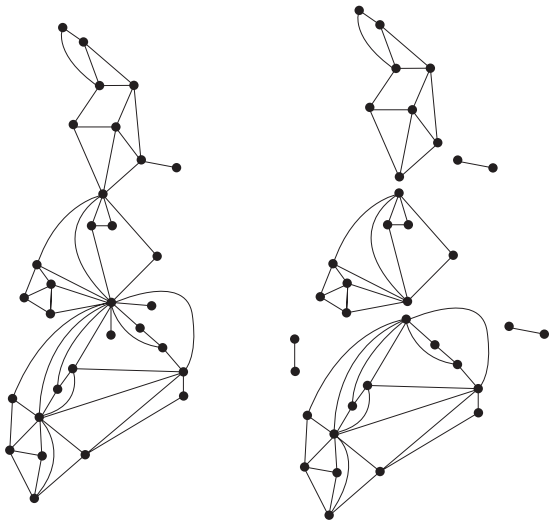

Figure 4. The landscape graph of Palmarola and its blocks.

vertex is connected to at least another vertex) can be disconnected by the removal of a single vertex or node termed as *cutnode.* Edges with the same cohesive property are termed as *bridges*. The fragments (nonseparable subgraphs) of a graph held together by its cutnodes and bridges are termed its *blocks* (Buckley and Harary 1990). Using our own example, the graph for the island of Palmarola (Figure 2) lies in six blocks with three cutnodes and three bridges connecting them (Figure 4). In ecological terms, the presence of cutnodes and bridges in the graph indicates that there could be barriers to dispersal between the disconnected blocks (Keitt et al. 1997).

Although indices of adjacency among patches are useful to quantify the local connectivity of a given landscape, they provide little insight into the connectivity structure of the entire landscape.

In transportation geography, overall network connectivity is measured by the gamma index, as the actual number of edges in the graph ($''\Sigma_i v_i$) divided by the number of edges of the corresponding planar graph, i.e., a graph with the maximum possible number of non-redundant pairwise connections assuming that no edge intersections are formed (Figure 5):

$$\gamma = \frac{\frac{1}{2}\sum_i v_i}{3(N-2)} \quad (2)$$

For the graph of Figure 1, we obtain $\gamma = 0.5$, whereas for the graph of Palmarola, $\gamma = 0.678$. In other words, the vegetation patches of Palmarola are connected to a relatively higher number of adjacent patches than the vegetation patches of the artificial landscape of Figure 1. Notice

that if different kinds of functional connections between patches are considered rather than spatial adjacency, then complete graphs (i.e., graphs where every pair of vertices is connected by an edge, Figure 6) may represent more adequate normalization terms for computing gamma connectivity.

The gamma index, however, only measures strict adjacency (touching) among vegetation patches without taking into account the effects between non-adjacent patches. A simple remedy of this drawback is to quantify network connectivity as the total topological distance in the graph (the number of all the edges between all pairs of vertices in the graph). This measure was first introduced by Wiener (1947) as the sum of the off-diagonal elements in the upper triangular distance submatrix of a given graph G:

$$W = \frac{1}{2}\sum_{i,j} d_{ij} \qquad (3)$$

Since $\mathbf{D}(G)$ is symmetric, the total distance of G (the sum of elements of the distance matrix) is simply twice the Wiener index W. Therefore, one can reduce the calculation of W to the upper triangular submatrix without loss of the properties of $\mathbf{D}(G)$. For example, for the artificial landscape of Figure 1, $W = 28$, whereas for the vegetation map of Palmarola, $W = 1305$.

The comparison of network connectivity between two landscapes with different numbers of landscape patches is possible by introducing relative connectivity indices. For instance, very simple formulae exist for computing W from chain graphs (Figure 7) and planar graphs (i.e., the least connected graphs and the most connected graphs, respectively) as a function of the number of vertices N:

$$W_{chain} = [N(N\text{-}1)/][(N\text{+}1)/3] \qquad (4)$$

$$W_{planar} = (N\text{-}2)^2 + 2 \; . \qquad (5)$$

Equation (4) was analytically derived by Bonchev and Trinajstic (1977). The conjecture behind Equation (5) is that, for any given number of vertices N, it is still possible to construct a planar graph where the topological distance d_{ij} between any pair of vertices that are not directly connected by one edge equals 2 (see Figure 5). As a consequence, for a planar graph, the number of elements in the upper triangular submatrix of $\mathbf{D}(G)$, $N(N\text{-}1)/2$, can be partitioned into a first set of $3(N\text{-}2)$ elements (i.e., the number of edges of the planar graph) where $d_{ij} = 1$, and a second set of $N(N\text{-}1)/2\text{-}3(N\text{-}2)$ elements where $d_{ij} = 2$.

It follows: $1 \times 3(N\text{-}2) + 2 \times [N(N\text{-}1)/2\text{-}3(N\text{-}2)] = (N\text{-}2)^2 + 2$. Notice however that this conjecture was simply verified with computer brute force and not analytically demonstrated. Counter examples may therefore still be possible. Following Equations (4) and (5), the Wiener index W of a graph G can be therefore normalized between 0 and 1 as:

$$\overline{W} = (W - W_{min}) / (W_{max} - W_{min}) = \\ = (W - W_{planar}) / (W_{chain} - W_{planar}) \qquad (6)$$

Connectivity has a trivial relationship to $\overline{W}$. Increasing connectivity for a given number of vertices N generally corresponds to shorter topological distances between vertices in the graph and to a lower value of $\overline{W}$. In our case, for the graph of Figure 1 $\overline{W} = 0.588$ and for the graph of Palmarola, $\overline{W} = 0.112$. Notice also that for complete graphs the Wiener index equals the number of elements

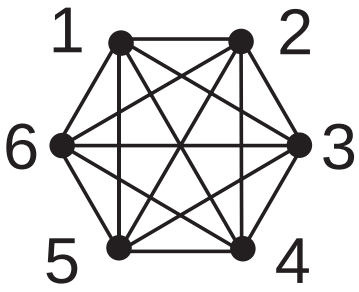

Figure 6. Complete graph with six vertices.

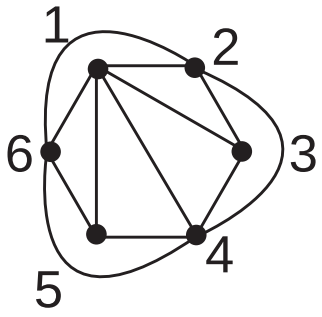

Figure 5. Planar graph with six vertices (i.e., the same number of vertices of the landscape graph of Figure 1).

Figure 7. Linear chain graph with six vertices.

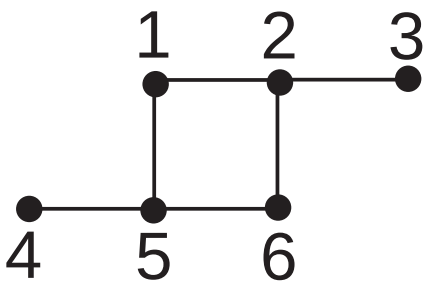

Figure 8. A graph with the same gamma connectivity (γ = 0.5) and Wiener index (W = 28) as the graph of Figure 1 but with a different Harary index (H = 9.917).

in the upper triangular submatrix of **A**(G) or **D**(G), i.e., $N(N\text{-}1)/2$.

Because gamma connectivity and the Wiener index are both calculated from integer entries either in the adjacency or in the distance matrix, they have a large degeneracy, i.e., several non-isomorphic graphs can correspond to the same W value (Devillers and Balaban 1999). In addition, the highest contribution to W is made by connections between topologically distant vertices. Conversely, a classical law of geography and landscape ecology holds that everything in a landscape is interrelated, but near patches are more related that distant ones (Forman and Godron 1986). In particular, the components of ecological systems such as species composition, biotic movement or fluxes of nutrient, water and energy are more greatly affected by neighboring patches (Acosta et al. 2000). Therefore, from an ecological viewpoint, the Wiener index is anti-intuitive. To remedy these two drawbacks in the computation of W, the distance matrix **D**(G) can be substituted by the reciprocal distance matrix **R**(G) with elements d_{ij}^{-1}. The sum of the off-diagonal values in the upper triangular submatrix of **R**(G) leads to a topological index termed the Harary index, H (Ivanciuc et al. 1993, Plavsic et al 1993). Since H is based on a summation of rational elements, it has a slightly lower degeneracy than W (Figure 8), while the highest contribution to H is made by connections between topologically close vertices in the graph. Within this context, the expressions for calculating the Harary index for chain and planar graphs assume the form:

$$H_{\text{chain}} = (N\text{-}1) + (N\text{-}2)/2 + (N\text{-}3)/3 + \ldots + 1/(N\text{-}1) \quad (7)$$

$$H_{\text{planar}} = N(N\text{+}5)/4 - 3 \quad (8)$$

whereas the expression for calculating H for a complete graph remains unchanged ($H_{\text{complete}} = N(N\text{-}1)/2$). Consequently, the expression for calculating the normalized Harary index $\overline{H}$ becomes:

$$\overline{H} = (H - H_{\text{chain}}) / (H_{\text{planar}} - H_{\text{chain}}) . \quad (9)$$

For our specific examples, the normalized Harary index is $\overline{H}$ = 0.236 (H = 9.833) for the artificial landscape of Figure 1 and $\overline{H}$ = 0.620 (H = 206.800) for the vegetation map of Palmarola. Notice that, unlike the normalized Wiener index, the normalized Harary index increases with increasing connectivity. We think therefore that $\overline{H}$ may be a better measure of landscape connectivity than more traditional indices such as gamma connectivity or the normalized Wiener index both from an intuitive and mathematical viewpoint.

Conclusions

Landscape graphs may be used for quantitatively describing a landscape as a series of spatially or functionally interconnected patches. In this sense, the Harary index H seems to be an effective index to quantify landscape network connectivity in a meaningful way. In ecological research, the relation between the Harary index and landscape connectivity may be of some significance for a better understanding of ecological processes, such as seed dispersal and gene flow across the landscape (Cantwell and Forman 1993). Furthermore, the normalized expression of H may offer a basis for graph theoretical comparison of landscape structures across space and time. However, it should be noted that, to date, the importance of TIs as a baseline to identify landscape structural properties that are relevant to critical ecological processes has yet to be convincingly illustrated. As is the case with other landscape indices (MacGarigal and Marks 1995, Riitters et al. 1995), the major shortcomings of TIs are that they are going to depend both on the classification scheme adopted for constructing the vegetation map and on the extent of the area analyzed. In addition, most TIs do not allow on principle any difference in quality (e.g., effect of different vegetation types) to be included in the calculation, and their relevance to ecological problems must be judged by the ecologist from the perspective of a certain ecological process (Molinari 1989, Schumaker 1996).

From a statistical viewpoint, by reducing graph topology into a single index, information is necessarily lost, and there is no ideal function capable of uniquely characterizing all aspects of landscape structure. Nevertheless, although different TIs have been defined to characterize different aspects of graph (landscape) structure, like connectivity, size, symmetry, circuitry, fragmentation, etc. based on distinct objectives and motivations, it is clear from the above that TIs share certain common features and a certain degree of intercorrelation (Basak et al. 1987). Future work is required to analyze the mutual relationships of published TIs to find a small set of non-re-

dundant metrics that span the important dimensions of landscape structure. Also, the possibilities of developing new "topoecological" indices that introduce qualitative differences among distinctive patches in the calculation of TIs are to be explored.

Acknowledgments: The authors wish to thank Alexandru Balaban, Subhash Basak, Mike Dale, János Podani, Bill Schwalm and two anonymous referees for the stimulating comments that substantially contributed improving this work.

References

Acosta, A., C. Blasi and A. Stanisci, A. 2000. Spatial connectivity and boundary patterns in coastal dune vegetation of central Italy. *J. Veg. Sci.*11: 149-154.

Basak, S.C., V.R. Magnuson, G.J. Niemi, R.R. Regal and G.D. Veith. 1987. Topological indices: thier nature, mutual relatedness, and applications. *Math. Modelling* 8:300-305.

Beier, P. and R.F. Noss. 1998. Do habitat corridors provide connectivity? *Conserv. Biol.* 12:1241-1252.

Blasi, C. 1994. Fitoclimatologia del Lazio. *Fitosociologia* 27:151-175.

Bonchev, D. and N. Trinajstic. 1977. Information theory, distance matrix and molecular branching. *J. Chem. Phys*. 67:4517-4533.

Buckley, F. and F. Harary. 1990. *Distance in Graphs.* Addison-Wesley, Reading, MA.

Cantwell, M.D. and R.T.T. Forman. 1993. Landscape graphs: Ecological modeling with graph theory to detect configurations common to diverse landscapes. *Landscape Ecol.* 8:239-255.

Cohen, J.E. 1978. Food Webs and Niche Space. Princeton University Press, Princeton, NJ.

Cohen, J.E., F. Briand and C.M. Newman. 1990. *Community Food Webs: Data and Theory*. Springer Verlag, New York.

Cosentino, D., M. Parotto and A. Praturlon. 1993. *Guide Geologiche Regionali: Lazio.* Società Geologica Italiana, Roma.

Couclelis, H. 1985. Cellular worlds: a framework for modeling micro-macro dynamics. *Environ. Plann.* A 17:585-596.

Davenport, D.W., D.D. Breshears, B.P. Wilcox and C.D. Allen. 1998. Sustainability of pińon-juniper ecosystems - a unifying perspective of soil erosion thresholds. *J. Range Manage*. 51:231-240.

Dale, M. 1985. Graph theoretical methods for comparing phytosociological structures. *Vegetatio* 63: 79-88.

Devillers, J. and A.T. Balaban. 1999. *Topological Indices and Related Descriptors in QSAR and QSPR.* Gordon and Breach, London.

Forman, R.T.T. and M. Godron. 1986. *Landscape Ecology.* Wiley, New York.

Grashof-Bokdam, C. 1997. Forest species in an agricultural landscape in the Netherlands: effects of habitat fragmentation. *J. Veg. Sci.* 8:21-28.

Grashof-Bokdam, C., J. Jansen and M.J.M. Smulders. 1998. Dispersal patterns of *Lonicera periclymenum* determined by genetic analysis. *Molecular Ecol.* 7:165-174.

Green, D.G. 1989. Simulated effects of fire, dispersal and spatial pattern on competition within vegetation mosaics. *Vegetatio* 82:139-153.

Green, D.G. 1994. Connectivity and complexity in landscapes and ecosystems. *Pacific Conserv. Biol.* 1:194-200.

Harary, F. 1969. *Graph Theory.* Addison-Wesley, Reading, MA.

Ivanciuc, O., T.S. Balaban and A.T. Balaban. 1993. Design of topological indices. Part 4. Reciprocal distance matrix, related local vertex invariants and topological indices. *J. Math. Chem.* 12:309-318.

Johnson, A.R., J.A. Wiens, B.T. Milne and T.O. Crist. 1992. Animal movements and population dynamics in heterogeneous landscapes. *Landscape Ecol.* 7:63-75.

Johnson, G., W. Myers, G.P. Patil and D. Walrath. 1998. Multiscale analysis of the spatial distribution of breeding bird species richness using the echelon approach. In: P. Bachmann, M Köhl and R. Päivinen (eds.), *Assessment of Biodiversity for Improved Forest Planning.* Kluwer Academic Publishers, Dordrecht, NL, pp. 135-150.

Keitt, T.H., D.L. Urban and B.T. Milne. 1997. Detecting critical scales in fragmented landscapes. *Conserv. Ecol.* [on line] 1(1): Art 4.

MacGarigal, K. and B.J. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. USDA Forest Service, Pacific Northwest Research Station, Genereal Technical Report PNW-GTR-351, Portland, OR.

Milne, B. T., A.R. Johnson, T.H. Keitt, C.A. Hatfield, J. David and P.T. Hraber. 1996. Detection of critical densities associated with pińon-juniper woodland ecotones. *Ecology* 77:805-821.

Molinari, J. 1989. A calibrated index for the measurement of evenness. *Oikos* 56:319-326.

Noss, R. F. 1991. Landscape connectivity: different functions and different scales. In: W.E. Hudson (ed.), *Landscape Linkages and Biodiversity.* Island Press, Washington, DC, pp. 27-39.

Pignatti, S. 1982. *Flora d'Italia. Edagricole*, Bologna, IT.

Plavsic, D., S. Nikolic, N. Trinajstic and Z. Mihalic. 1993. On the Harary index for the characterization of chemical graphs. *J. Math. Chem.* 12:235-250.

Riitters, K.H., R.V. O'Neill, C.T. Hunsaker, J.D. Wickham, D.H. Yankee, S.P. Timmins, K.B. Jones and B.L. Jackson. 1995. A factor analysis of landscape pattern and structure metrics. *Landscape Ecol.* 10:23-39.

Risser, P.J., J.R. Karr and R.T.T. Forman. 1984. *Landscape Ecology: Directions and Approaches.* Special Publication 2. Illinois Natural History Survey, Champaign, IL.

Roberts, D.W. 1989. Analysis of forest succession with fuzzy graph theory. *Ecol. Model.* 45:261-274.

Schippers, P. J. Verboom, J.P. Knaapen and R.C. van Apeldoorn. 1996. Dispersal and habitat connectivity in complex heterogeneous landscapes: an analysis with a GIS-based random walk model. *Ecography* 19:97-106.

Schumaker, N.H. 1996. Using landscape indices to predict habitat connectivity. *Ecology* 77:1210-1225.

Stanisci, A. and M. Pezzotta. 1992. Trasformazioni nel paesaggio vegetale delle isole Ponziane (Lazio, Italia centrale). *Colloques Phytosociologiques* 21:489-509.

Sugihara, G. 1984. Graph theory, homology and foods webs. *Proc. Symp. Appl. Math.* 30:83-101.

Taaffe, E.J. and H.L. Gauthier Jr. 1973. *Geography of Transportation.* Prentice-Hall, Englewood Cliffs, NJ.

Turner, M.G., R.H. Gardner, V.H. Dale and R.V. O'Neill. 1989. Predicting the spread of disturbance across heterogeneous landscapes. *Oikos* 55:121-129.

Wiener, H. 1947. Structural determination of paraffin boiling point. *J. Amer. Chem. Soc.* 69:17-20.